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Sexual activity reduces lifespan of male fruitflies

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Many theories on the evolution of life histories have assumed a physiological cost of reproduction in terms of reduced lifespan[1–3]. A cost of increased reproduction in terms of reduced longevity has been established experimentally for females, both as an additive genetic[4,5] and as a purely phenotypic[6,7] effect. Such a physiological cost of reproduction has not been demonstrated for males. The cost of sexual activity has been assumed to be relatively small in those species where the only paternal contribution to an offspring is the gamete[8,9]. Here we show that increasing sexual activity reduces longevity in the male fruitfly (*Drosophila melanogaster*) and hence that there is a significant physiological cost of male sexual activity in a species where the father contributes only gametes to his progeny.

The flies used were an outbred stock collected in Dahomey in 1970. Sexual activity was manipulated by supplying individual males with receptive virgin females at a rate of one or eight virgins per day. The longevity of these males was recorded and compared with that of two control types. The first control consisted of two sets of individual males kept with newly inseminated females equal in number to the virgin females supplied to the experimental males. Newly inseminated females will not usually re-mate for at least 2 days[10,11] thus they served as a control for any effect of competition with the male for food or space. The second control was a set of individual males kept with no females. There were 25 males in each of the experimental and control groups, and the groups were treated identically in respect of number of anaesthetizations (using CO_2) and provision of fresh food medium.

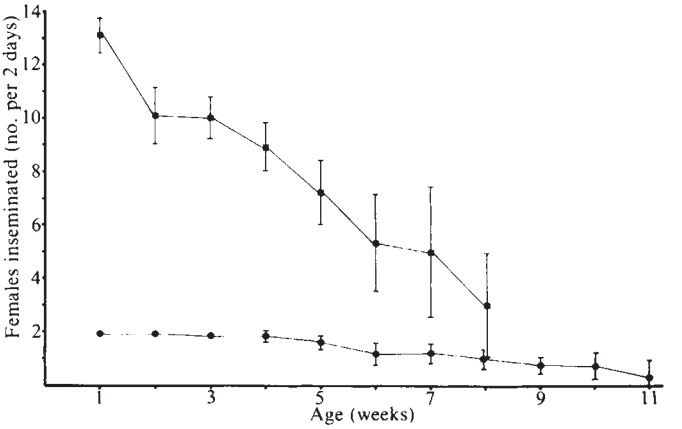

Fig. 1 The relationship between insemination rate (number of females inseminated per 2 days) and age (weeks) for males kept with one virgin female (●) or eight virgin females (■) per day. Error bars are 95% confidence limits.

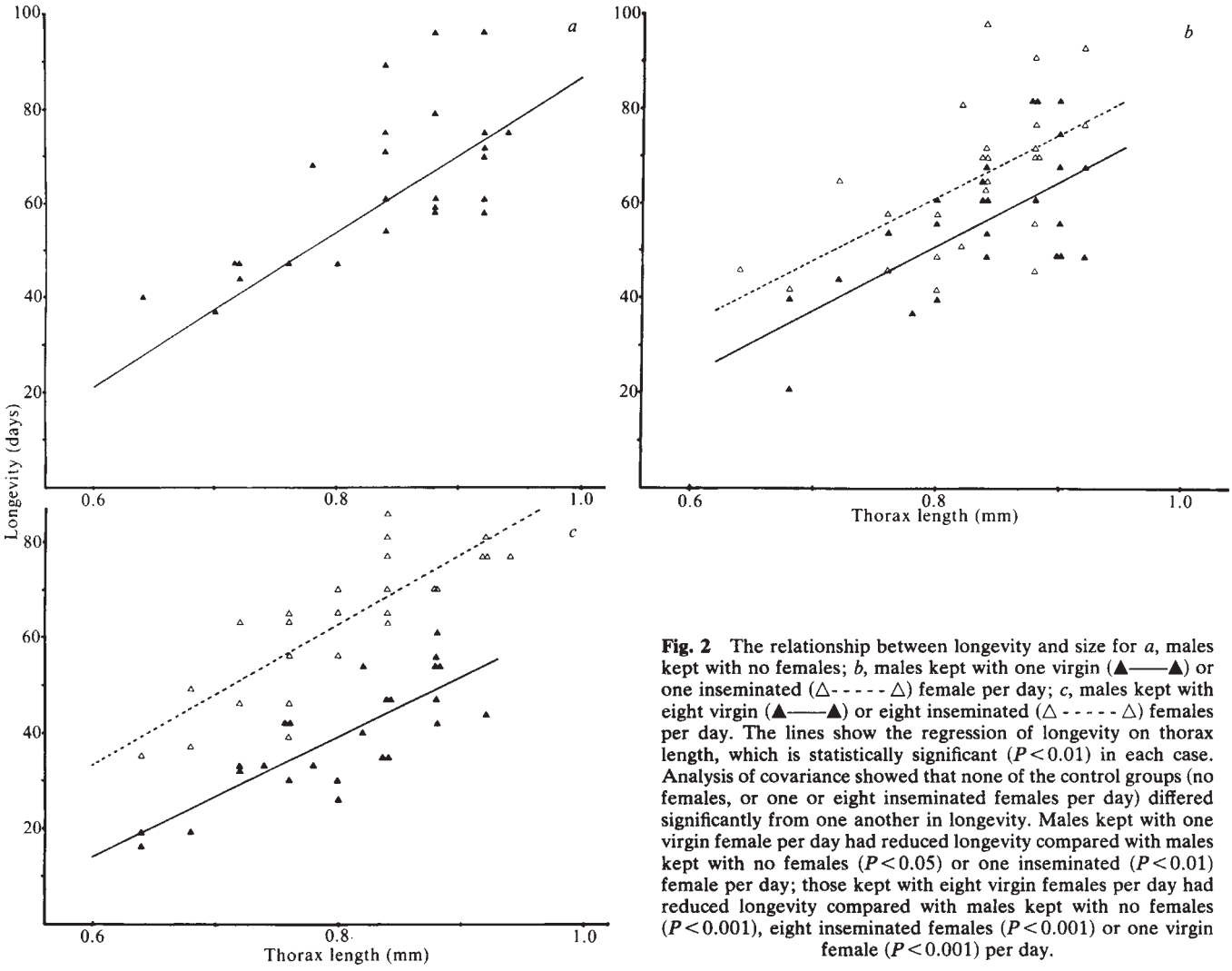

Fig. 2 The relationship between longevity and size for *a*, males kept with no females; *b*, males kept with one virgin (▲——▲) or one inseminated (△- - - - -△) female per day; *c*, males kept with eight virgin (▲——▲) or eight inseminated (△ - - - - -△) females per day. The lines show the regression of longevity on thorax length, which is statistically significant ($P<0.01$) in each case. Analysis of covariance showed that none of the control groups (no females, or one or eight inseminated females per day) differed significantly from one another in longevity. Males kept with one virgin female per day had reduced longevity compared with males kept with no females ($P<0.05$) or one inseminated ($P<0.01$) female per day; those kept with eight virgin females per day had reduced longevity compared with males kept with no females ($P<0.001$), eight inseminated females ($P<0.001$) or one virgin female ($P<0.001$) per day.

On two days per week throughout the life of each experimental male, the females that had been supplied as virgins to that male were kept and examined for fertile eggs. This gave an estimate of the insemination rate of the two groups of males (Fig. 1). In both groups the insemination rate declined with the age of the male, and the rate was higher for males supplied with eight virgins per day than for those supplied with only one virgin per day. There were no significant differences in insemination rate between the individual males within each experimental group.

In the absence of any sexual activity, the longevity of male fruitflies is associated with their size (Fig. 2*a*). Size was therefore taken into account when examining the effect of sexual activity on longevity (Fig. 2*b*, *c*). Analysis of covariance showed that: (1) there were no significant differences in longevity between the control groups (median longevity 65 days); (2) the males supplied with one virgin female per day had significantly reduced longevity (median 56 days) compared with males in any control group; (3) males kept with eight virgin females per day had significantly reduced longevity (median 40 days) compared with males kept with one virgin female per day, and control males. These results show that male sexual activity reduces longevity, and that this effect is more marked for a higher level of sexual activity.

Physiological costs of particular activities have generally been discussed in terms of the diversion of nutrients into these activities at the expense of others[12]. In our experiment, energetic costs of sexual activity would have included the production of sperm and seminal fluid and the muscular action associated with mating itself. In addition to inseminating females, the experimental males probably also performed higher levels of courtship than control males. The control males kept without females performed no courtship. When inseminated females are courted they extrude the ovipositor, which terminates the male courtship[13]. In nature, nutritional effects may be increased by food shortage, and there may be costs of sexual activity in addition to those detected here. Searching for mates[14] and fighting with other males[15] may be costly physiologically and these activities, together with courtship and mating, may make males more vulnerable to predation[16].

Sexual activity could affect longevity in two ways. First, it may have an effect on the probability of death occurring in the next short period of time. Cessation of sexual activity at any age would then leave a fly with a life expectancy comparable with that of controls of the same age. High temperatures can have such an effect on longevity in *Drosophila subobscura*[17]. Second, sexual activity may have some cumulative, possibly irreversible, effect. Williams[18] has suggested that senescence may be caused by the deleterious pleiotropic effects later in life of genes which have beneficial effects early in life. A deleterious long-term effect of sexual activity earlier in life could produce such a pleiotropic effect. Phenotypic correlations of the kind found in these experiments need not necessarily mean that a genetically caused change in the level of male sexual activity would alter longevity. A negative additive genetic correlation would be needed to demonstrate this and should be the subject of further experiments.

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